GAMANTHERA (LAURACEAE), A NEW GENUS FROM COSTA RICA[1]

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ABSTRACT

A new genus of the Lauraceae, *Gamanthera*, is described from Costa Rica. It is distinguished from all other Lauraceae by its completely fused stamens, forming a synandrium, with only three, two, or one locellus, and by its monoecious nature.

During the past few years, intensive collecting efforts in Costa Rica have resulted in a great number of additions to the *Flora Costaricensis*, as well as in a number of undescribed taxa. Several new species of Lauraceae have recently been published (Hammel, 1986; Burger, 1988; van der Werff, 1988; Zamora et al., 1988), and 14 species were published in the treatment of the Lauraceae for the *Flora Costaricensis* (Burger & van der Werff, 1990). Burger (1988) published a new genus, *Povedadaphne*, from Costa Rica and noted that recently five mostly South American genera had been added to the known flora of Costa Rica. Recent fieldwork organized under the auspices of the Manual Flora of Costa Rica project, organized by the Missouri Botanical Garden, has yielded another Lauracea from Costa Rica, which is here described as a new, monotypic genus. The surge of new taxa of Lauraceae from Costa Rica can be attributed to the unusual richness of its flora, but perhaps a more likely explanation for these discoveries is the excellence of the Costa Rican botanists participating in the botanical exploration of their country. It is, therefore, with pleasure that we name the new species after Gerardo Herrera, who discovered it and whose excellent collections of Lauraceae have given us much pleasure to work with.

Gamanthera herrerae van der Werff, gen. et sp. nov. TYPE: Costa Rica. Alajuela, Upala, Colonia Puntarenas, along Río Chimuria, tree, 8 m, flowers yellowish, fruits green, cupule pink, 11 Nov. 1987, *Herrera 1228* (holotype, MO; isotypes, BM, CR, HBG, US). Figure 1.

Arbores monoeciae. Folia alterna, venatione pinnata. Gemmae conspicue bracteatae. Inflorescentiae axillares, paniculatae, basi bracteis vel cicatricibus bractearum praeditae, ex floribus solum masculinis vel femineis constantes. Flores masculini synandrio tribus staminibus perfecte connatis facto. Synandrium 3, 2, vel 1-locellatum. Fructus cupulae duplimarginatae insidens.

Tree, 8 m tall. Twigs terete, densely brown-tomentellous, with occasional whorls of scars from fallen bracts. Axillary and terminal buds conspicuous, covered by several whorls of bracts, the small basal bracts brown-pubescent outside, the large inner bracts glabrous or nearly so, but with ciliate margins; inner surface of bracts glabrous. Leaves alternate, chartaceous, 12–20 × 5–8 cm, elliptic, margin undulate, the base cuneate to broadly cuneate, the apex shortly acuminate, the acumen to ca. 1 cm long; upper surface of mature leaves with midrib tomentellous, especially near the base, otherwise glabrous, young leaves with a rather dense indument of short (0.2–0.3 mm), erect hairs; lower surface with midrib and lateral veins brown-tomentellous, the lamina with erect pubescence, hairs ca. 0.3 mm long; lateral veins 5–8 on each side, arching upward near the margin, not or very weakly loop-connected, venation immersed or nearly so on upper surface, midrib and lateral veins prominently raised on lower surface, tertiary venation also raised. Petioles terete, brown-tomentellous, 1–1.5 cm (rarely to 2 cm) long, adaxially flattened, abaxially terete. Inflorescences axillary, brown-tomentose, paniculate, to 7 cm long, with bracts or scars of fallen bracts at the base, flowers clustered near the tips of the secondary or very short tertiary axes, rarely solitary, not cymosely arranged; axes

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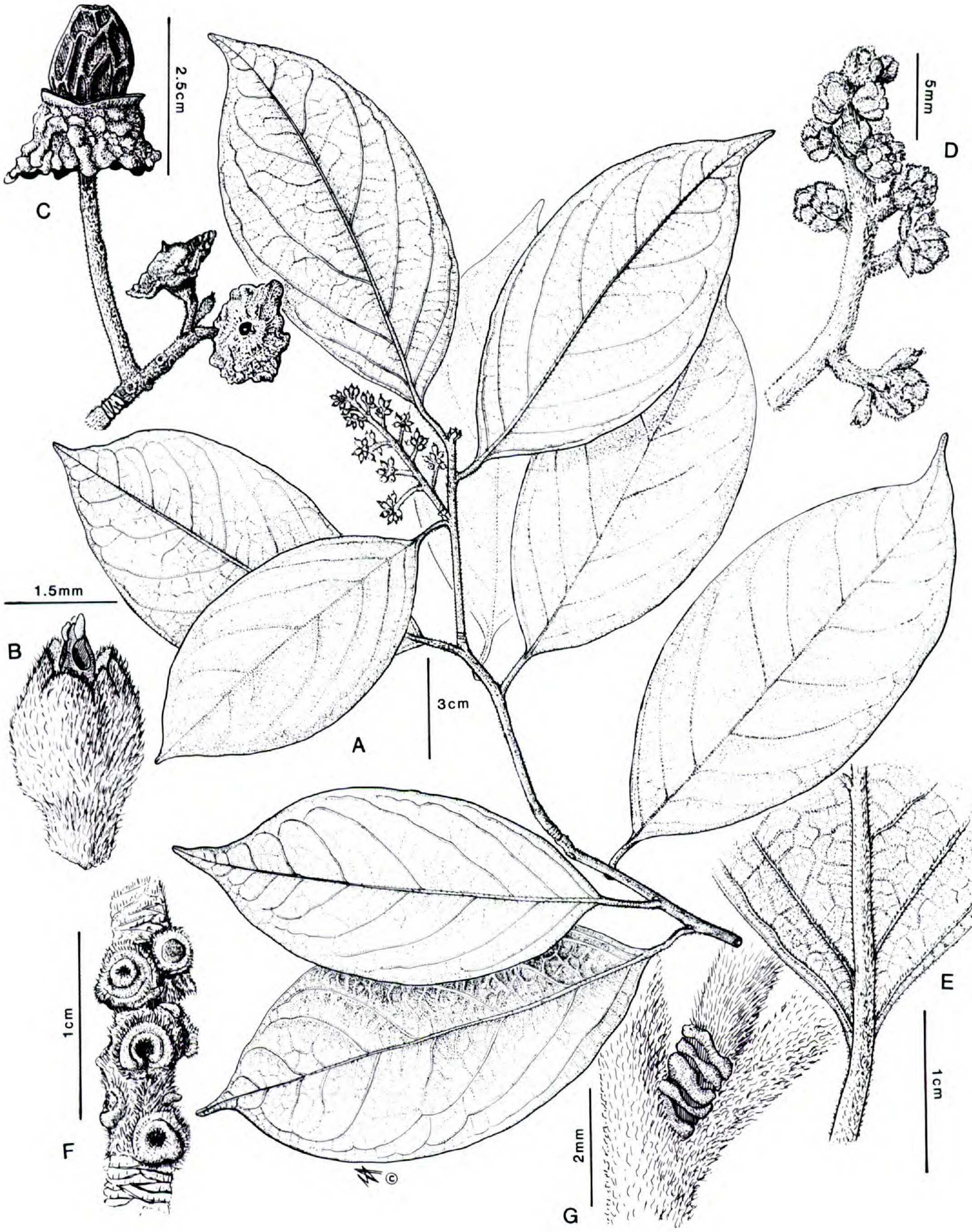


FIGURE 1. *Gamanthera herrerae*.—A. Habit.—B. Flower.—C. Young and old fruits, the young ones enclosed in the cupule, the old one exserted.—D. Detail of inflorescence.—E. Base of leaf, showing indument.—F. Detail of stem, showing linear scars from fallen bracts and circular scars from fallen buds.—G. Base of axillary inflorescence, showing linear scars from fallen bracts.

and flowers subtended by bracts, these broadly to narrowly ovate-elliptic, to 2.5 mm long or, when fallen off, by a scar. Inflorescences with either staminate or pistillate flowers. Flowers sessile or nearly so, unisexual, 4–4.5 mm long, including the narrowed base; staminate and pistillate flowers externally very similar; tepals 6, erect, broadly triangular, pubescent outside, the free part to 1.5

mm long, inner 3 tepals shorter than outer 3. Staminate flowers with a central, narrowly conical synandrium formed by fusion of 3 stamens (Fig. 2), the fusion complete and individual stamens not recognizable, the synandrium 2 mm long, the glabrous anther-bearing part and the densely pubescent fused filaments each 1 mm long; locelli 3, 2, or infrequently 1; staminodia and pistillode lacking. Pollen grains globose, inaperturate, spinulose (Fig. 3). Bisexual flowers with a one-sided(?) synandrium; ovary situated beside(?) the synandrium, glabrous, narrowly ellipsoid, gradually narrowed into a slender, long style (Fig. 4). Receptacle glabrous inside. Stigma not seen. Fruit ellipsoid, ca. 1.5 cm long, the exserted part 1 cm long, cupule deeply cupshaped, double-rimmed, the undulate-lobed outer margin strongly reflexed.

Paratype. Collected from same tree as type specimen, *Grayum et al. 9039* (CR, F, LE, MEXU, MO, S, USJ, Z).

Anatomy of the Staminate Flower

MATERIAL AND METHODS

Figures 5 and 6 were prepared by P. Endress. Pickled flowers of the collection *Grayum 9039* were examined with the scanning electron microscope (SEM) after critical point drying and sputter coating with Au/Pd. Other samples were used for microtome serial sections and stained with safranin and astra blue. Figures 2–4 were prepared by H. van der Werff. Dried flowers were dissected without rehydration and sputter coated with Au.

RESULTS

The perianth consists of two trimerous whorls of tepals (Fig. 8). The androecium in the center of the flower consists of a massive conical body which bears one to three pollen sacs at its top (Figs. 7, 9, 10, 11). Nectaries are lacking. At anthesis the flower does not expand and retains the globular shape of the bud (Fig. 5). Only the upper part of the androecium with the pollen sacs protrudes through the small opening of the flower and is exposed (Fig. 6). Each pollen sac opens by a flap, which is hinged at the top and recurves toward the top (Figs. 5, 6). The flap is shorter than the pollen sac and does not extend to its base (Fig. 11C). The diagrammatic position of the pollen sacs is opposite the inner tepals (Fig. 8). The androecium is always served by three collateral vascular bundles irrespective of the number of pollen sacs (Fig. 11A–C). In androecia with three pollen sacs the vascular bundles alternate with the pollen sacs (Fig. 11C). The bundles are situated toward the center of the androecium and terminate somewhat above the lower end of the pollen sacs (Fig. 11C).

DISCUSSION—INTERPRETATION OF THE ANDROECIUM

How is this highly unusual androecium to be interpreted? Normal stamens of Lauraceae are served by a single vascular bundle situated in the center of the stamen behind the two pollen sacs (if the anther is bilocular), as seen in a transverse section. Here, in *Grayum 9039*, there are three vascular bundles, which suggest three stamens. The three vascular bundles alternate with the tepals of the inner whorl. In lauraceous taxa, where the androecium is reduced to a single whorl, e.g., in *Licaria* (cf. Mez, 1889, as *Misanteca*; Kostermans, 1957) or *Mezilaurus* (van der Werff, 1987), the stamens alternate with the tepals of the inner whorl.

From this it follows that the conical androecium consists of three stamens that are completely congenitally fused into a compact synandrium. If three pollen sacs are differentiated, each "anther" consists of two "half" pollen sacs in that the two neighboring pollen sacs of two stamens have merged into one. Merger of two pollen sacs of different thecae (or at least of their flaps) into one functional unit also occasionally occurs in other lauralian groups; e.g., in *Siparuna* the two flaps of an anther may merge into one (here, two thecae of the same anther) (cf. Endress & Hufford, 1989).

The male flowers of *Grayum 9039*, therefore, represent an extremely reduced stage previously unknown in the Lauraceae. In other taxa with bisexual flowers reduction of the androecium to one stamen whorl, which is congenitally fused into a tube surrounding the gynoecium, is the ultimate stage so far known. This is the case in species of *Licaria* (Kostermans, 1957; as *Misanteca* in Mez, 1889) and *Mezilaurus* (van der Werff, 1987). In *Kubitzkia* there are still three staminal whorls, whereby the third is connate into a tube (as *Systemonodaphne* in Kostermans, 1957). Fusion of the filaments of whorls II and III occurs in an undescribed species of *Rhodostemonodaphne* (van der Werff, pers. obs.). However, the anthers remain free in all of these cases.

In *Grayum 9039*, congenital fusion of the remaining three stamens into a massive (compact) central body and fusion of neighboring pollen sacs of neighboring stamens, reduction of pollen sac

fig.2

fig.4

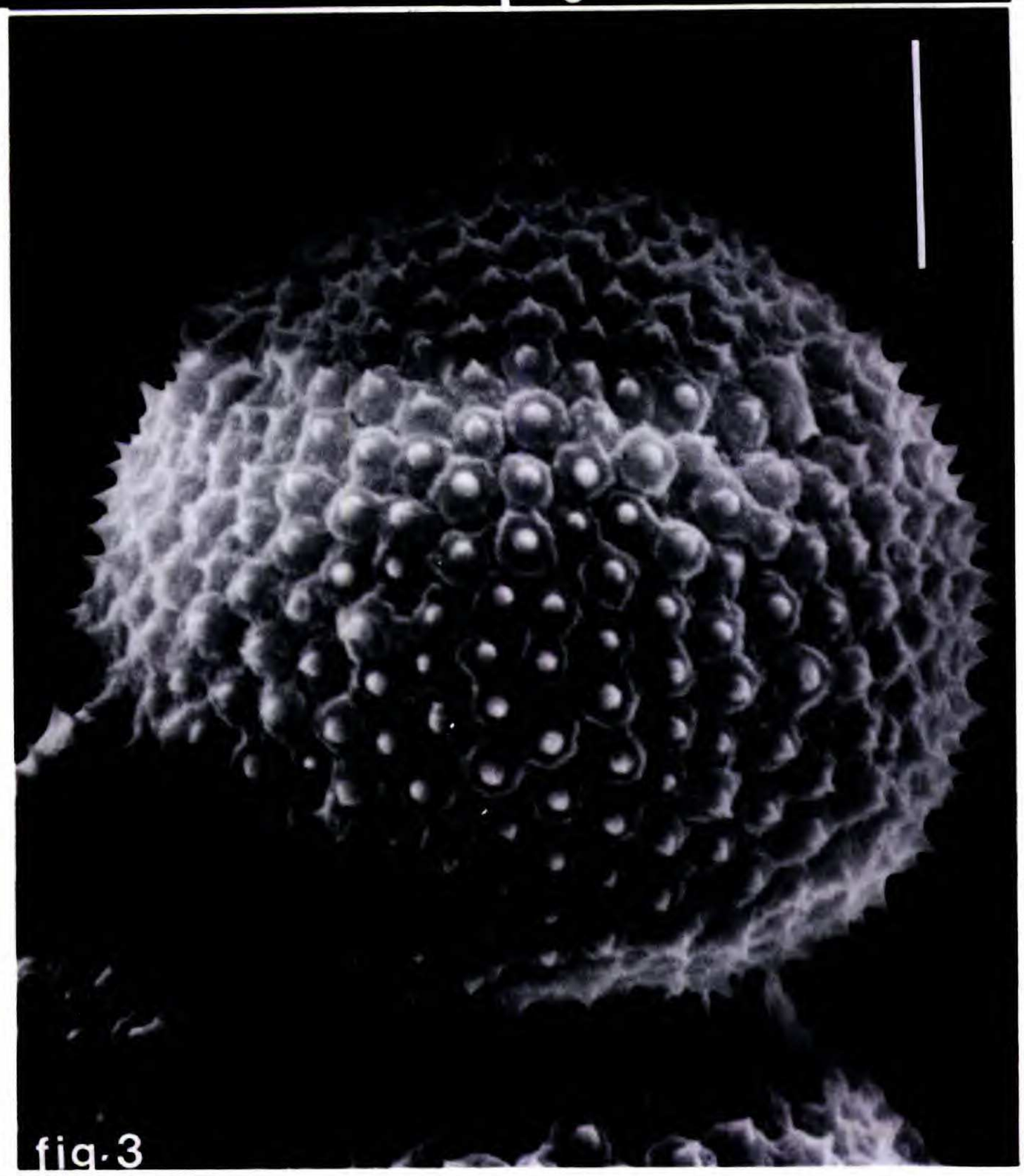
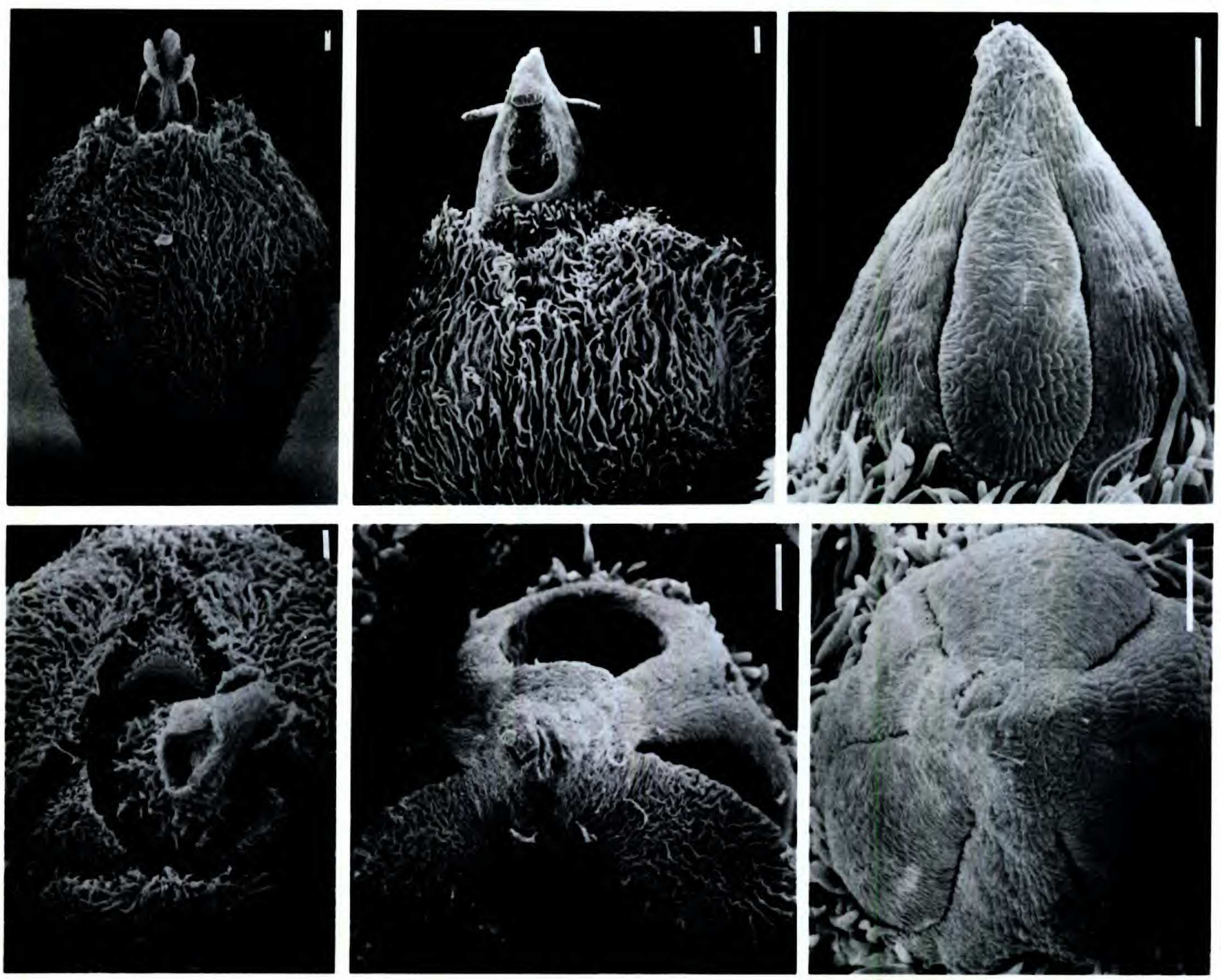


fig.3



FIGURES 5–10. SEM micrographs of flowers and pollen of *Grayum 9039*. Scale bars = 0.1 mm.—5. Open flower from the side, two open pollen sacs visible.—6. Upper half of open flower, three open pollen sacs visible—7. Synandrium from the side, three closed pollen sacs with the dehiscence lines of the flaps visible.—8. Open flower from above, the six tepals and the synandrium with the three open pollen sacs visible.—9. Synandrium from above, three open pollen sacs visible; the flap of the uppermost pollen sac has been removed.—10. Synandrium from above, three closed pollen sacs visible.

number to two or one in some flowers, and loss of the nectary appendages, represent a further step in this trend of reduction within the Lauraceae.

Synandry is relatively frequent in Magnoliidae. Because the shape of the stamens is more or less bulky, synandry is relatively easy to establish from a morphogenetical point of view, mainly in unisexual flowers, where a gynoecium is lacking as a potential obstacle in the floral center (Endress, 1989).

DISCUSSION

Gamanthera herrerae is currently known only from the vicinity of Upala in the Alajuela Province, Costa Rica. The two collections were made in con-

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FIGURES 2–4. SEM micrographs of flowers and pollen of *Grayum 9039*.—2. Dissected male flower, showing the synandrium.—3. Pollen grain.—4. Dissected female flower, showing glabrous ovary below the synandrium and the slender style; part of the synandrium removed to show style. Scale bars in Figures 2 and 4 = 0.5 mm; in Figure 3 = 0.005 mm.

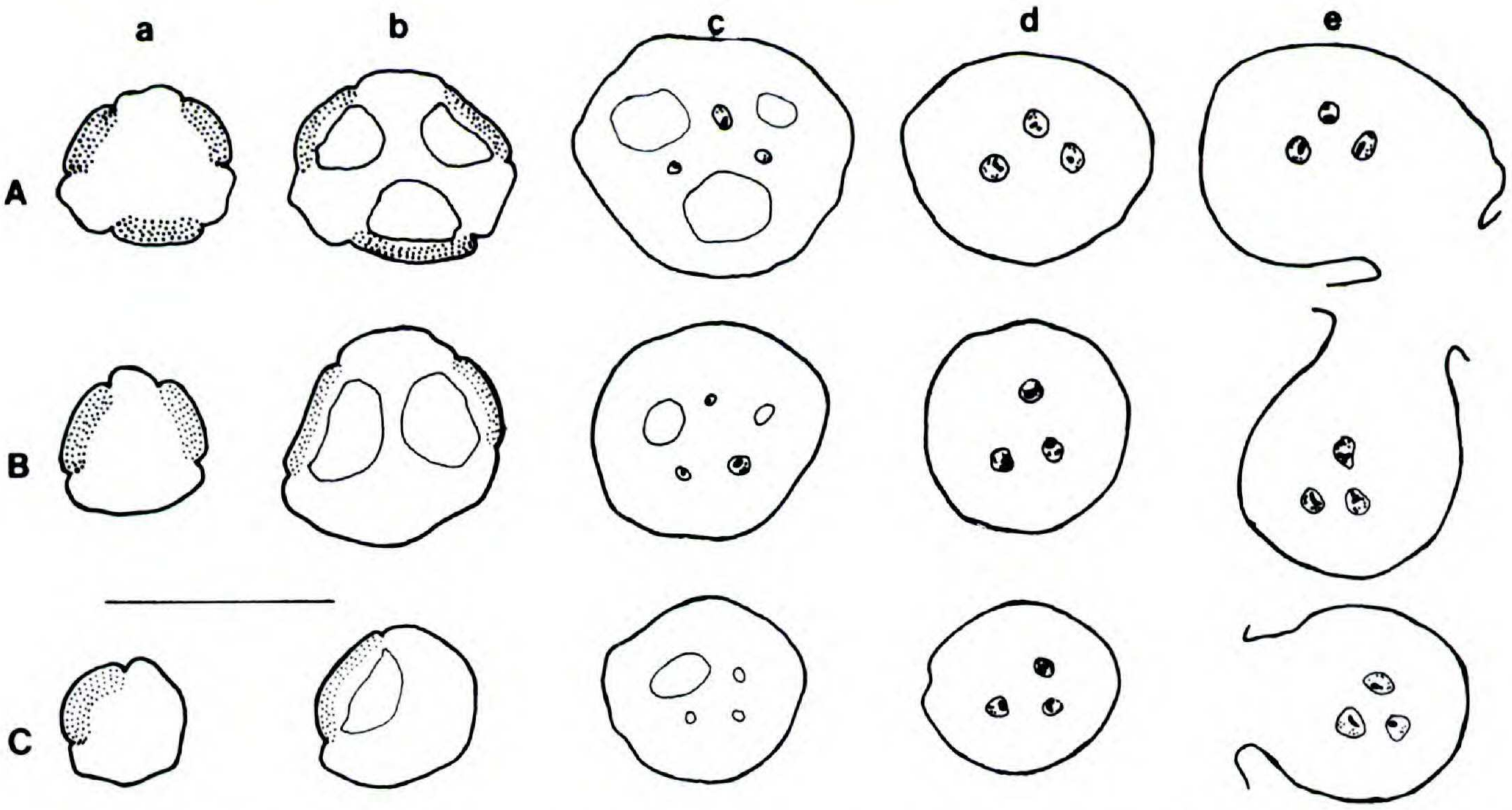

FIGURE 11. Microtome serial transverse sections of synandria of three male flowers of *Grayum 9039*. Scale bar = 0.5 mm. Endothecium of the pollen sacs stippled. In vascular bundles xylem black, phloem stippled.—A. Synandrium with three pollen sacs.—B. Synandrium with two pollen sacs.—C. Synandrium with one pollen sac. (a) Sections at upper end of pollen sacs. (b) Sections at middle level of pollen sacs. (c) Sections at base of pollen sacs. (d) Sections below pollen sacs. (e) Sections at base of synandrium.

secutive years from the same tree. A search in the vicinity yielded only two additional trees, one sterile, the other juvenile. The trees were not large, but hard to find; it is likely that, if one would be willing to spend a week searching, more trees could be located.

Several inflorescences contain deformed flowers infested by insect larvae. Such flowers have basal, spreading tepals and a central, depressed-globose, densely pubescent growth. This growth probably represents the deformed synandrium, as is indicated by the densely pubescent surface. The locelli-bearing part of the synandrium is usually present, but always more or less lateral, never at the tip of the growth. The deformed flowers have a hollow center, which usually contain an insect larva. Such flowers were only found in the male inflorescences and never contained a trace of an ovary. Infructescences with "young fruits" are part of all specimens. These "young fruits" are almost completely included in a broad, flat-topped cupule (the two righthand "fruits" in Fig. 1C). Upon dissection these "fruits" show an absence of a well-defined outer wall and a seed; instead they are filled with nondifferentiated tissue which contains a few, irregular cavities. Although we did not find larvae in these "fruits," we consider them abnormalities, probably caused by insect or mite activity. The lefthand fruit in Figure 1C is not abnormal; it has the distinct outer wall found in other Lauraceae and contains a shrivelled, dried seed. The two collections of *Gamanthera* include only one normal fruit but several dozen of the abnormal "young fruits."

This new genus possesses several features that are either unknown or very rare in neotropical Lauraceae. The most striking of these is the androecium, which consists of three completely fused stamens, as is described above. Staminodia have not been found, nor are there glands associated with the synandrium. A complete fusion of stamens, including anthers, has not previously been reported for Lauraceae. This synandrium, which is located in the center of the flower, appears to be a single stamen and only a study of the vascularization showed its true origin. The number of locelli on the synandrium can be three, two, or one; one synandrium with four locelli was found with the locelli arranged in two horizontal pairs, the septum separating the two locelli of one pair much thinner than the walls separating the pairs.

A second unique feature in *Gamanthera* (at least for Lauraceae) is the presence of two flower types on the same tree. Lauraceae have either bisexual or unisexual flowers; if unisexual flowers are present, the species are dioecious. In most cases, the unisexual character of the flowers can be readily seen, but in some species (for instance, in *Ocotea*,

van der Werff, pers. obs.) the reduction of the nonfunctional organs in the flower is not obvious, and it can be difficult to decide whether flowers are unisexual or bisexual. Howard (1981) reported that some species of *Ocotea* s.l. were found to be polygamodioecious, with perfect and functionally unisexual flowers present in the same inflorescence, an observation we have not been able to confirm. The first collection of *Gamanthera* included inflorescences and young fruits, sometimes with the inflorescence and fruit attached to the same twig. The inflorescences consisted of only staminate flowers, without even a trace of a gynoecium. After much searching, pistillate flowers were found on the infructescences as old, dried flowers. Seven flowers of different infructescences were dissected and these were all pistillate. The pistillate flowers are, without dissection, indistinguishable from the staminate flowers and possess a similar synandrium. The synandrium often persists on young fruits. We did not find pollen grains in the synandria of the pistillate flowers, but have not found pollen grains in synandria with opened valves of staminate flowers either. Pollen was only found in flowers with the synandrium still included in the flower and valves closed. Thus, it is possible that the flowers described as pistillate are bisexual and that *Gamanthera* has unisexual (staminate) and bisexual flowers on separate inflorescences on the same plant, rather than pistillate and staminate flowers on separate inflorescences on the same plant. Either way, this is a situation not previously recorded for Lauraceae. It is not yet clear how pollinization takes place. In the pistillate flowers the ovary is fully covered by the synandrium. In contrast to the staminate flowers, the synandrium of the pistillate flowers is hollow and the style ascends through the hollow core (Fig. 4). The style can be followed up to the level of the locelli, where it seems to disappear. A pore in the synandrium through which a stigma can penetrate has not been found. Such a pore is likely present in younger flowers, but might become unrecognizable in old flowers. The pistillate flowers seen are only present on infructescences and are likely several months old. On the twig that carries a staminate inflorescence and an infructescence, the infructescence is attached much lower on the twig than the inflorescence. In *Gamanthera* it is difficult to estimate the age of the flowers, as there are, apart from the elongation of the synandrium, no changes in size or shape. The general trend in Lauraceae is that staminate flowers fall off soon after shedding their pollen. Because young staminate flowers (in which synandria are still enclosed in the flowers and locelli have not opened) are present on some specimens, the staminate flowers are probably not very old. On the other hand, the development of the cupules on the infructescences suggests that these pistillate inflorescences are much older. Therefore, it seems likely that the pistillate and staminate flowers on the available specimens have quite different ages, and it is not certain that staminate and pistillate flowers are simultaneously functional on the same tree. If this is not the case, *Gamanthera* could be an interesting example of dichogamy in a monoecious species with unisexual flowers. Dichogamy has been reported for Lauraceae in genera with perfect flowers (Stout, 1927; Kubitzki & Kurz, 1984) and seems widespread in the family.

A third interesting feature of *Gamanthera* is the series of bracts surrounding the inflorescence and vegetative buds. Once inflorescences and twigs grow out of the buds, the bracts fall off and leave clusters of linear scars at the base of the inflorescence and young twigs. Clusters of scars on twigs occur in several genera of neotropical Lauraceae (*Aniba*, *Endlicheria*, *Mezilaurus*, *Pleurothyrium*, van der Werff, pers. obs.). Species in these genera with bracts all have leaves clustered near the tips of their branches, and the bracts are narrowly elliptic with an acute tip and frequently with a rudimentary midrib, quite unlike the broad, scalelike bracts found in *Gamanthera*. In *Persea schiedeana*, another species with clustered leaves, the bracts surrounding the vegetative buds are broad and scalelike, but this species lacks bracts at the base of the inflorescences. The only genus in the Neotropics with scalelike bracts surrounding the vegetative buds and with alternate leaves (apart from *Gamanthera*) is *Litsea*, which occurs at high elevations from Mexico to Costa Rica. In *Litsea* the flowers are arranged in pseudo-umbels, which are subtended by scalelike bracts. It is likely that these bracts represent the floral bracts, which, like the flowers, have become greatly condensed. In *Gamanthera*, floral bracts are present in addition to the bracts at the base of the inflorescence, and these latter bracts seem unique among neotropical Lauraceae.

RELATIONSHIPS

Infrafamilial classification of Lauraceae (Kostermans, 1957; Hutchinson, 1964) is based on the following characters: presence or absence of bracts (or decussate bracts surrounding the subumbellate inflorescences), development of cupule, number of fertile stamens, and number of anther cells. The characters found in *Gamanthera* do not agree with

any of the tribes as defined by these authors. Monoecious trees with inflorescences composed of flowers of one sex only had not been reported before in Lauraceae. The bracts at the base of the inflorescences suggest a relationship with the Laureae, but against this argue the facts that in the Laureae the bracts subtend the (mostly subumbellate) flowers, not the common peduncle, as in *Gamanthera*; that in the Laureae inflorescences are subumbellate or racemose, not paniculate as in *Gamanthera*; and that in Laureae the cupule is never double-margined. The other tribes are defined by cupule and androecial characters. The highly reduced androecium of *Gamanthera* precludes placement in any of these tribes. Probably the closest is the subtribe Anibineae of Kostermans (1957), which includes genera with double-margined cupules and some fusion of stamens (but never to the degree found in *Gamanthera*). Against the placement of *Gamanthera* in the Anibineae are the bracts surrounding the inflorescences and vegetative buds, and the monoecious condition. In favor of a relationship with Anibineae is the fact that Anibineae are well represented in the Neotropics, whereas Laureae include only one neotropical species.

The pollen of *Gamanthera* (Fig. 3) is globose, inaperturate, and spinulose, and agrees with the general pollen characteristics of neotropical Lauraceae (Raj & van der Werff, 1988). Diameter of the grains is about 20 μ and the spinules are seated on cushionlike bases, these without granular processes. These characters agree well with the Anibineae and do not indicate a relationship with the Laureae.

H. G. Richter (pers. comm.) reported that the wood of *Gamanthera* is nondescript and typical of Lauraceae; the bark corresponds with Richter's (1981) *Licaria* type 1, *Aniba*, and *Ocotea* pro parte. These conclusions rule out a relationship of *Gamanthera* with the Laureae and place it somewhere in the Anibineae. A close relationship with *Mezilaurus*, which includes some species with fused filaments of the three stamens, is not likely because *Mezilaurus* differs in its wood characters (Richter, 1981), clustered leaves, and small, platelike cupules. Instead, *Gamanthera* might be closer related to *Licaria*, although we consider *Gamanthera* distinct from *Licaria* because of its synandrium and clusters of bracts along twigs and at base of inflorescences. The relationships between genera of Lauraceae are presently not well understood and are in need of much further study.

Literature Cited

Burger, W. C. 1988. A new genus of Lauraceae from Costa Rica with comments on problems of generic and specific delimitation within the family. Brittonia 40: 275–282.

——— & H. van der Werff. 1990. Lauraceae. *In:* W. C. Burger (editor), Flora Costaricensis. Fieldiana, Bot., n.s. 23: 1–129.

Endress, P. K. 1989. Evolution of reproductive structures and functions in primitive angiosperms (Magnoliidae). Mem. New York Bot. Gard. 55: 5–34.

Endress, P. K. & L. D. Hufford. 1989. The diversity of stamen structures and dehiscence patterns among Magnoliidae. Bot. J. Linn. Soc. 100: 45–85.

Hammel, B. E. 1986. New species and notes on Lauraceae from the Caribbean lowlands. J. Arnold. Arbor. 67: 123–136.

Howard, R. A. 1981. Nomenclatural notes on the Lauraceae of the Lesser Antilles. J. Arnold Arbor. 62: 45–61.

Hutchinson, J. 1964. The Genera of Flowering Plants. Clarendon Press, Oxford.

Kostermans, A. J. G. H. 1957. Lauraceae. Commun. Forest Res. Inst. 57: 1–64.

Kubitzki, K. & H. Kurz. 1984. Synchronized dichogamy and dioecy in neotropical Lauraceae. Pl. Syst. Evol. 147: 253–266.

Mez, C. 1889. Lauraceae Americanae. Jahrb. Königl. Bot. Gart. Berlin 5: 1–556.

Raj, B. & H. van der Werff. 1988. A contribution to the pollen morphology of neotropical Lauraceae. Ann. Missouri Bot. Gard. 75: 130–167.

Richter, H. G. 1981. Anatomie des sekundaeren Xylems und der Rinde der Lauraceae. Sonderb. Naturwiss. Vereins Hamburg 5: 1–148.

Stout, A. B. 1927. The flower behavior of Avocados. Mem. New York Bot. Gard. 7: 145–203.

Werff, H. van der. 1987. A revision of *Mezilaurus* (Lauraceae). Ann. Missouri Bot. Gard. 74: 153–182.

———. 1988. Eight new species and one new combination of neotropical Lauraceae. Ann. Missouri Bot. Gard. 75: 402–419.

———. 1991. New species of Lauraceae from Ecuador and Peru. Ann. Missouri Bot. Gard. 78: 409–423.

Zamora, N., L. Poveda & E. Canessa. 1988. Una nueva especie de *Caryodaphnopsis* Airy Shaw (Lauraceae) para la región neotropical. Ann. Missouri Bot. Gard. 75: 1160–1166.